

Archaeoteleia Masner in the Cretaceous and a new species of Proteroscelio Brues (Hymenoptera, Platygastroidea)

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Abstract

The generic concepts of *Archaeoteleia* Masner and *Proteroscelio* Brues are expanded to accommodate two new species that are here described: *Archaeoteleia astropulvis* Talamas **sp. n.** and *Proteroscelio nexus* Talamas **sp. n.** A specimen of *Archaeoteleia* from Baltic amber is illustrated and discussed. Diagnoses of *Proteroscelio*, *Proterosceliopsis* Ortega-Blanco, McKellar & Engel and *Bruescelio* Ortega-Blanco, McKellar & Engel, a key to Cretaceous platygastroid genera with 14-merous antennae, and a key to the species of *Proteroscelio* are presented.

Keywords

amber, fossil, *Archaeoteleia*, *Bruescelio*, *Proteroscelio*, *Proterosceliopsis*

Introduction

This work was catalyzed by two platygastroid specimens in Burmese amber brought to the National Museum of Natural History by Longfeng Li, a visiting student from Capitol Normal University, Beijing, during her study on fossil Hymenoptera. Both inclusions are exceptionally well preserved, and upon close examination, the specimens warrant expansion of the concepts of the genera to which they belong: *Proteroscelio* Brues and *Archaeoteleia* Masner. The former is only known from Cretaceous amber (Brues 1937, Johnson et al. 2008), while the latter has, until now, only been known from extant specimens in South America and New Zealand (Masner 1968, Early et al. 2007).

The generic placement of *Archaeoteleia astropulvis* Talamas exemplifies the importance of understanding the extant fauna of a taxon to interpret fossils. We place *A. astropulvis* in *Archaeoteleia* without reservation, but over the course of 100 million years, *Archaeoteleia* has changed enough that a novice might not recognize the characters that unite the fossil with extant species. This is particularly relevant because *A. astropulvis* does not fully comply with a generic concept of *Archaeoteleia* based solely on extant specimens (Early et al. 2007). Through examination of this specimen we discovered a new character that is found throughout *Archaeoteleia*, the form of the anterior mesepisternal area, which we use to reinforce the generic concept. Such union of fossil and extant morphologies is especially illuminating and requires examination of *both* kinds of specimens.

Proteroscelio nexus Talamas expands the range of morphological diversity found in *Proteroscelio* and reduces the number of characters that separate *Proteroscelio* from *Bruescelio* Ortega-Blanco, McKellar & Engel and *Proterosceliopsis* Ortega-Blanco, McKellar & Engel.

As summarized in Talamas et al. (2015), dates of lineages are increasingly being utilized to understand the evolutionary history of groups with dating algorithms that rely on accurate taxonomy for proper calibration. *Archaeoteleia astropulvis* extends the age of *Archaeoteleia* ~100 million years into the past and confirms that it retains plesiomorphic characters, as was first posited by Masner (1968).

Materials and methods

The numbers prefixed with “USNMENT” or “OSUC ” are unique identifiers for the individual specimens (note the blank space after some acronyms). The specimens in Burmese amber were given “USNMENT” collecting unit identifiers, and are also referenced by CNU collection numbers. Both identifiers are presented in the Material Examined sections. Details on the data associated with these specimens may be accessed at the following link: purl.oclc.org/NET/hymenoptera/hol, and entering the identifier in the form. Persistent URIs for each taxonomic concept were minted by xBio:D in accordance with best practices recommended by Hagedorn et al (2013).

Morphological terms were matched to concepts in the Hymenoptera Anatomy Ontology (Yoder et al 2010) using the text analyzer function. A table of morphological terms and URI links is provided in Suppl. material 1.

Taxonomic synopses and matrix-based descriptions were generated from the Hymenoptera Online Database (hol.osu.edu) and the online program vSysLab (vsyslab.osu.edu) in the format of character: state.

Photographs were captured with a Z16 Leica[®] lens with a JVC KY-F75U digital camera using Cartograph[®] software, or a Leica[®] DMRB compound microscope with a GT-Vision[®] Lw11057C-SCI digital camera attached. In both systems, lighting was achieved using techniques summarized in Buffington et al. (2005), Kerr et al. (2009) and Buffington and Gates (2009). Single montage images were produced from image stacks with the program CombineZP[®]. In some cases, multiple montage images were stitched together in Photoshop[®] to produce larger images at high resolution and magnification. Full resolution images are archived at the image database at The Ohio State University (specimage.osu.edu).

Dissections for scanning electron microscopy were performed with a minuten probe and forceps and body parts were mounted to a 12 mm slotted aluminum mounting stub (EMS Cat. #75220) using a carbon adhesive tab (EMS Cat. #77825-12) and sputter coated with approximately 70 nm of gold/palladium using a Cressington[®] 108auto sputtercoater. Micrographs were captured using a Hitachi[®] TM3000 Table-top Microscope at 15 keV.

Author contributions

EJT: photography, manuscript preparation, character analysis, taxonomy; NFJ: taxonomic analysis, manuscript preparation; database development and maintenance; MLB: manuscript preparation; DR: provision of specimen.

Collections

This work is based on specimens deposited in the following repositories with abbreviations used in the text:

CASC	California Academy of Science, San Francisco, USA
CCHH	Hoffeins Collection, Hamburg, Germany
CNCI	Canadian National Collection of Insects, Ottawa, Canada
CNU	Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Shanghai, China
OSUC	C.A. Triplehorn Collection, The Ohio State University, USA
USNM	National Museum of Natural History, Washington, DC, USA

Character annotations

1Rs	first abscissa of the radial sector vein (Figure 22)
2Rs	second abscissa of the radial sector vein (Figure 22)
ama	anterior mesepisternal area (Figures 8–10, 13, 15)
b	bullae (Figures 5–6, 17)
bs	basiconic sensillum (Figure 21)
eps	episternal foveae (Figure 9)
M	median vein (Figure 22)
not	notaulus (Figure 22)
occ	occipital carina (Figure 22)
pes	postepomial sulcus (Figures 7, 9)
pshs	pronotal suprahumeral sulcus (Figures 7, 9)
pss	posterior scutellar sulcus (Figure 22)
pssu	prespecular sulcus (Figure 7)
sasu	subacroleural sulcus (Figures 7–8)
tpc	transverse pronotal carina (Figures 7, 9)
ts	tibial spur (Figures 5, 16)

Results

Concept of *Archaeoteleia*

To evaluate the morphology of extant *Archaeoteleia* we examined 14 species directly: (*A. araucana* Masner, *A. chambersi* Early, *A. dispar* Masner, *A. gilbertae* Early, *A. karere* Early, *A. mellea* Masner, *A. novazealandiae* Masner, *A. onamata* Early, *A. penai* Masner, *A. puncticeps* Masner, *A. pygmea* Masner, *A. robusta* Masner, *A. simulans* Masner and *A. submetallica* Masner) in addition to the images presented in the revision by Early et al. (2007).

We place *A. astropulvis* in *Archaeoteleia* based on the presence of 2 tibial spurs on the metatibia, venation of the fore wing, the sulci along the anterior margins of T2–T4 and S2–S4, and the form of the anterior mesepisternal area. The distal apices of the mesotibiae are not clearly visible and although we did not observe them directly, we suspect that there are two mesotibial spurs as in all other *Archaeoteleia*.

The following characters presented by Early et al. (2007) can no longer be treated as ubiquitous for *Archaeoteleia*: A3 the longest antennomere in females, episternal foveae absent, and the number of mandibular teeth (2 teeth in extant species, 3 in *A. astropulvis*). The characteristic shape of the clypeus in extant species was used by Early et al. (2007) as a generic character. The clypeus in the holotype specimen of *A. astropulvis* is obscured, precluding assessment of this character. However, based on the position of the interantennal process relative to the mandibles, we assume that the clypeus is much shorter than in extant species.

During the course of this study we encountered a male specimen in Baltic amber (Figures 15–18) that we tentatively identify as *Archaeoteleia*. The observable morphology is consistent with the concept of *Archaeoteleia* in Early et al. (2007), including the wing venation (Figure 17) and the presence of two tibial spurs on the hind tibia (Figure 16). Only the dorsal margin of the anterior mesepisternal area is clearly visible, and it is carinate (Figure 15) as in other macropterous specimens of *Archaeoteleia*. The metasoma is entirely occluded by a hole drilled through the amber and the ventral portion of the head is not visible. The description of *Electroteleia* Brues by Johnson et al. (2008) states that this genus has tyloids on the male antennomeres A4–A8. The specimen of *Archaeoteleia* illustrated in Figures 15–18 has a tyloid only on A5, consistent with the description of *Archaeoteleia* by Early et al. (2007). Despite the incompleteness of this specimen's visible morphology, we consider it useful to bring attention to it because other relevant specimens are likely present in Baltic amber collections and may shed light on the evolution of *Archaeoteleia*.

Character discussion

Antenna

Figure 3 (*A. mellea*) illustrates a distinctly elongate A3, which is typical for extant *Archaeoteleia*. However, even among extant species, this character exhibits significant variation. Figure 4 illustrates the head and antennae of a female of *A. pygmea*: A3 is the longest antennomere, but by a much smaller degree than in *A. mellea* and its length is of the same order of magnitude as A2. Because of this plasticity, we do not use relative antennomere length to exclude *A. astropulvis*, in which A3 is shorter than A2 and only slightly longer than A4, from *Archaeoteleia*.

Wing Venation

The degree to which the marginal vein is sclerotized differs significantly between *A. astropulvis* and from extant species and *Archaeoteleia* in Baltic amber (compare Figures 5–6, 17).

Anterior mesepisternal area

In all species of *Archaeoteleia*, the anterior mesepisternal area is elevated relative to the surrounding mesopleuron and has carinate posterior margins. The posterodorsal margin of the anterior mesepisternal area corresponds with anterior limit of either the subacropleural sulcus or the prespecular sulcus. The posteroventral margin aligns with the episternal foveae (when foveae are present). We examined this character in

representatives of more than 100 platygastroid genera across all subfamilies and major lineages and found that the anterior mesepisternal area is clearly delimited and present as a raised area in only a handful of genera outside of *Archaeoteleia*: *Cremastobaeus* Ashmead, *Dyscritobaeus* Perkins, *Mecix* Masner, *Pseudanteris* Fouts, *Scelio* Latreille, *Synoditella* Muesebeck, *Telenomus* Haliday and *Thoron* Haliday. In none of these are the posterior limits of the anterior mesepisternal area sharply margined by carinae as in *Archaeoteleia*.

Sexual dimorphism

The anterior mesepisternal area in the micropterous females of *Archaeoteleia pygmea* and apterous females of *A. submetallica* is a simple carina along the anterior margin of the mesopleuron (Figure 14). In the macropterous males of *A. pygmea* (Figure 11) the anterior mesepisternal area is fully developed in the form typical for the genus. The episternal foveae are an attachment site for the mesopleuro-mesobasale muscle (Mikó et al. 2007), and thus it is unsurprising that microptery is associated with reduction in this character. The nature of the musculature, if any, associated with the subacropleural and prespecular sulci is presently unknown to us. We consider the form of the anterior mesepisternal area to be a generic character for *Archaeoteleia*, albeit one that is subsequently modified in micropterous or apterous females.

Episternal foveae

Contrary to Early et al. (2007), conspicuous episternal foveae are commonly encountered in *Archaeoteleia* (Figure 9).

Pronotal shoulder

Some species of *Archaeoteleia* have two distinct sulci dorsal to the transverse pronotal carina. When both sulci are present, we refer to the sulcus along the dorsal margin of the pronotum as the pronotal suprahumeral sulcus, and the sulcus directly along the dorsal margin of the transverse pronotal carina as the postepomial sulcus.

Archaeoteleia astropulvis Talamas, sp. n.

<http://zoobank.org/870E09B4-7E5B-4074-BD5D-3A8C293F0227>

http://bioguid.osu.edu/biod_concepts/407676

Figures 1–2, 5, 10

Description. Female body length: 1.62 mm (n=1).



Figure 1. *Archaeoteleia astropulvis*, female holotype (USNMENT01109982), habitus, ventrolateral view. Scale bars in millimeters.

Head. Number of mandibular teeth: 3. Malar sulcus: present. Malar striae: present. Facial striae: present. Lengths of flagellomeres: approximately equal to maximal width. Number of clavomeres: 6. Frontal depression: absent. Hyperoccipital carina: absent. Number of antennomeres: 12. Orbital carina: absent. Swelling along inner orbit of compound eye: present. Occipital carina: absent below midpoint of compound eye.

Mesosoma. Netrion sulcus: complete, indicated by line of circular foveae. Pronotal cervical sulcus: indicated by deep circular foveae. Posterior pronotal sulcus: absent. Sculpture of lateral pronotum: smooth in ventral half, weakly rugulose dorsally. Transverse pronotal carina: present. Epomial carina: absent. Transverse pronotal carina: present. Setation of lateral axillar region: absent. Macrosculpture of mesoscutum: absent. Notaulus: percurrent. Macrosculpture of mesoscutellum: absent. Spines on mesoscutellar disc: absent. Mesepimeral sulcus: extending along length of posterior margin of mesopleuron, dorsally continuous with cells of prespecular sulcus. Episternal foveae: present, extending from acetabular carina to base of mesopleural carina. Postacetabular sulcus: present as a smooth furrow. Prespecular sulcus: indicated by shallow crenulae extending posteriorly from anterior mesepisternal area. Anterior mesepisternal area: present. Sculpture of mesopleuron below femoral depression: smooth. Sculpture of femoral depression: smooth. Mesopleural carina: present anteriorly, effaced posteriorly.



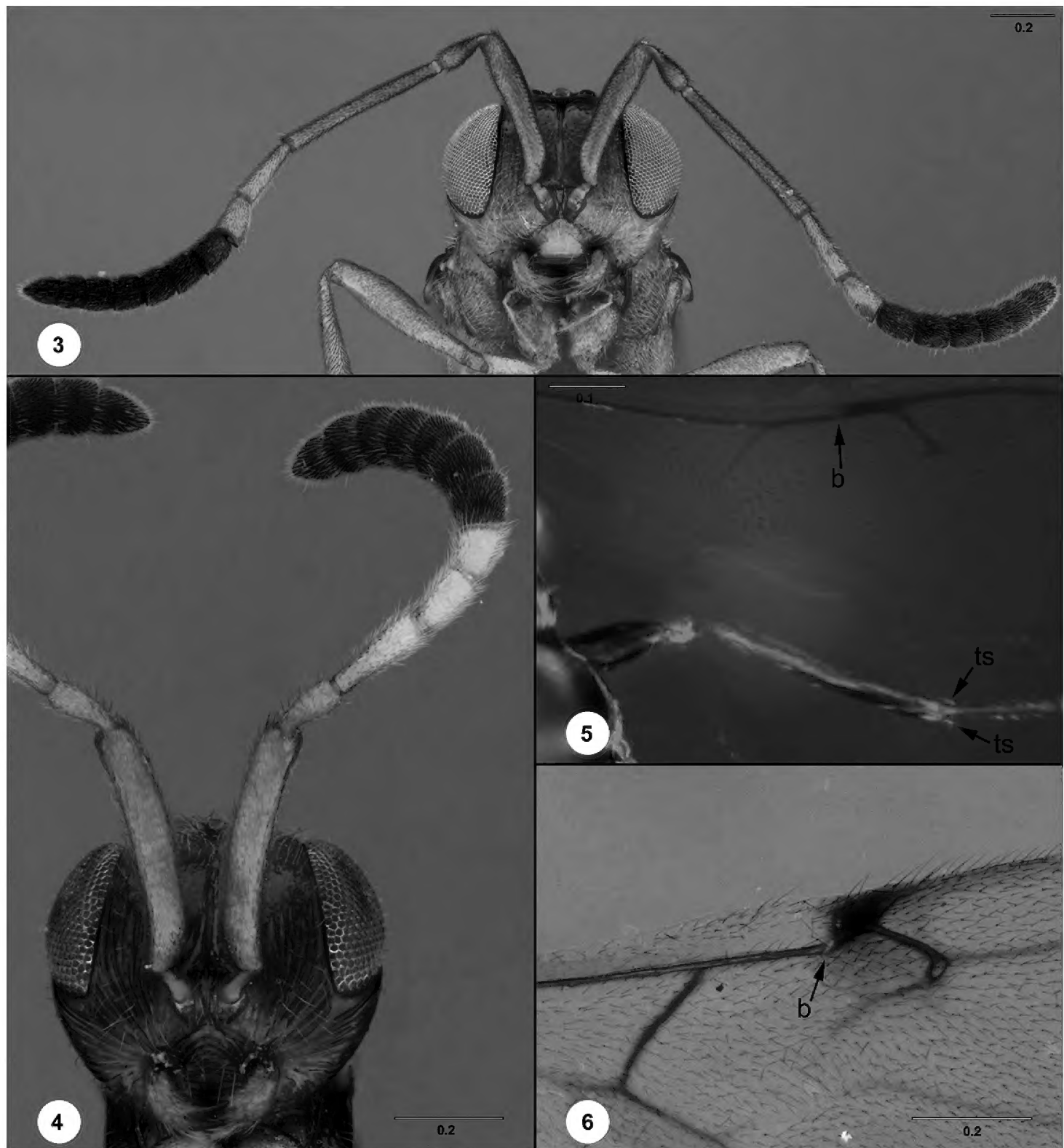
Figure 2. *Archaeoteleia astropulvis*, female holotype (USNMENT01109982), habitus, dorsolateral view. Scale bars in millimeters.

Paracoxal sulcus: indicated by line of foveae. Sculpture of dorsal metapleuron: smooth.

Posterior projection of the propodeum: present, visible only in lateral view due to bubble in amber. Length of postmarginal vein: about 2.7 times as long as stigmal vein. Length of marginal vein: about equal to length of stigmal vein. Bristles on submarginal vein in fore wing: absent. Basal vein in fore wing: present as a nebulous line. Bulla: present.

Metasoma. Felt fields on S2: absent. Sculpture of S2–S5: smooth posterior to cells of antecostal suture. Sculpture of T2–T5: smooth posterior to cells of antecostal suture. Horn on T1: present. Antecostal sutures on sternites: indicated by large cells on S2–S4. Antecostal sutures on tergites: indicated by cells on anterior T2–T4.

Diagnosis. *Archaeoteleia astropulvis* can be separated from females of extant species by multiple characters. A2 and A3 are distinctly elongate in extant species (Figures 3–4) and in *A. astropulvis* the length of these antennomeres is approximately equal to their width. The mandibles are bidentate in extant species and tridentate in *A. astropulvis*. Lastly, in extant macropterous species, the marginal vein is thickly sclerotized into a “stigma” whereas in *A. astropulvis* the marginal vein is simple.

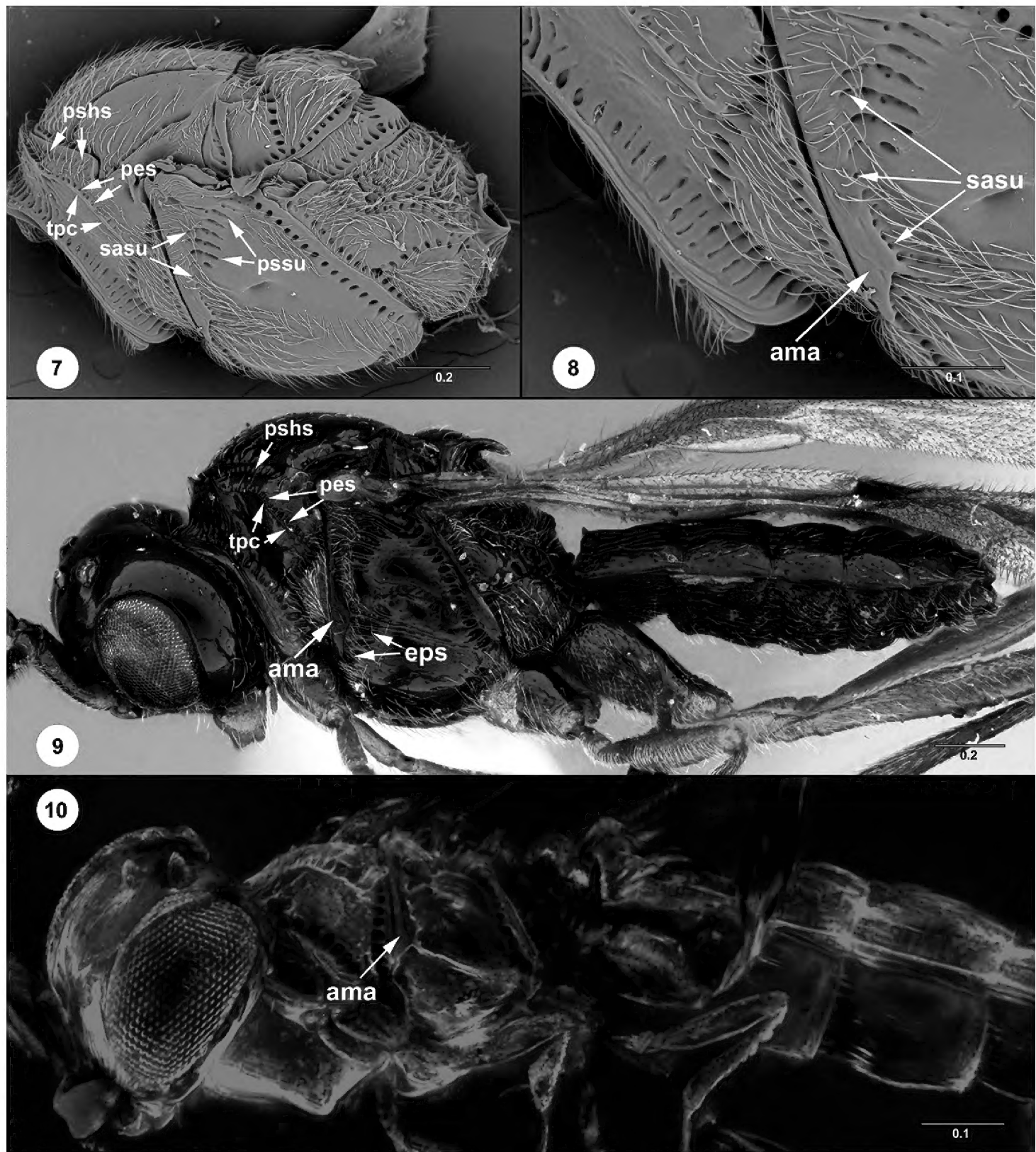


Figures 3–6. **3** *Archaeoteleia mellea*, female (OSUC 203348), head and antennae, anterior view **4** *A. pygmaea*, female (146602), head and antennae, anterior view **5** *Archaeoteleia astropulvis*, female holotype (USNMENT01109982), fore wing and metatibia, dorsal view **6** *Archaeoteleia gracilis*, male (OSUC 163002), fore wing venation. Scale bars in millimeters.

Etymology. This species epithet “astropulvis” is a Latin translation of “star dust”, that refers to the ancient source of the atoms that form our planet and its inhabitants and commemorates the late David Bowie alter ego, Ziggy Stardust. It is treated as a noun in apposition.

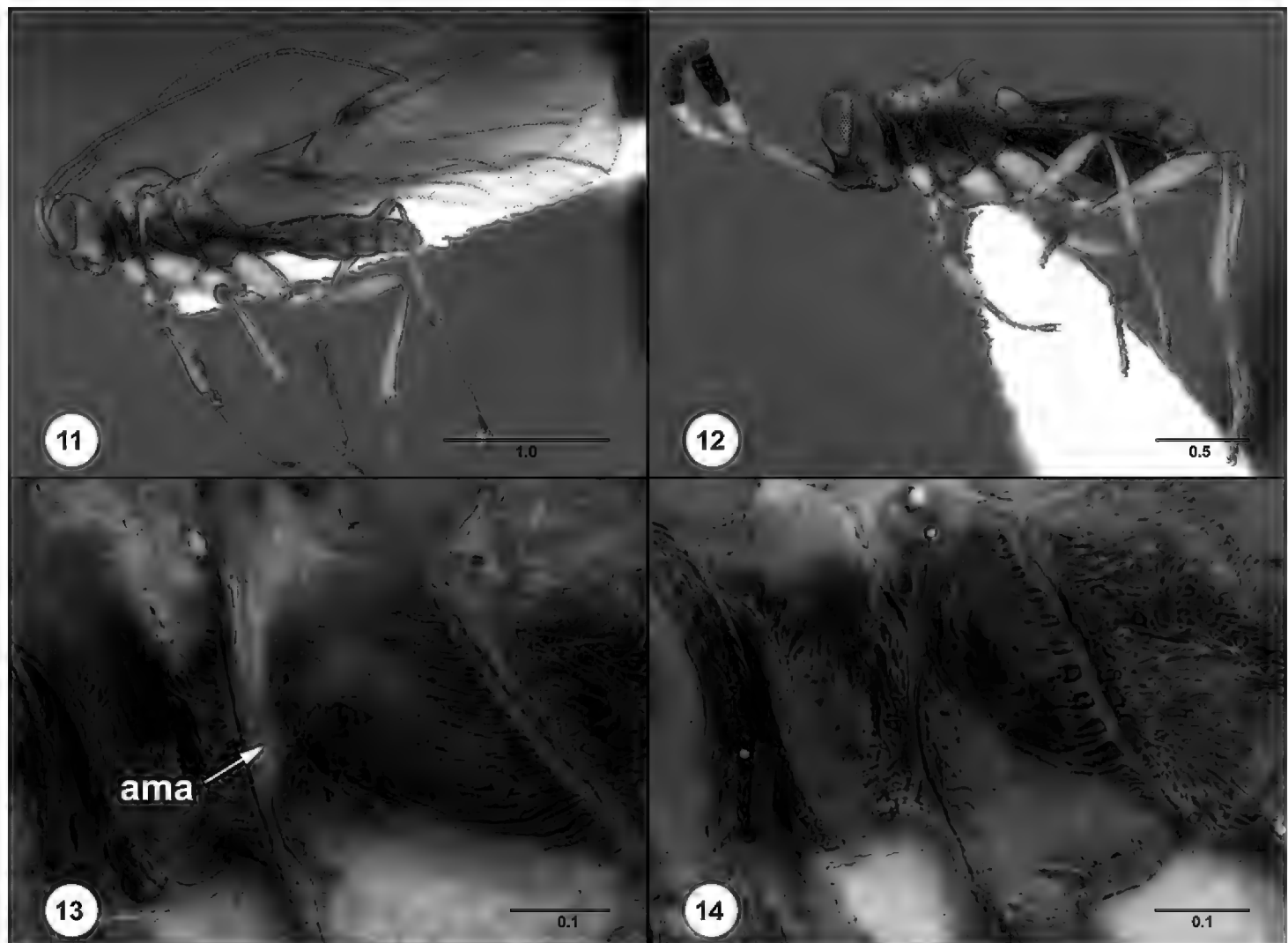
Link to distribution map. <http://hol.osu.edu/map-large.html?id=407676>

Material examined. Holotype, female: **MYANMAR:** CNU-HYM-MA-2014014 (USNMENT01109982) (deposited in CNU).



Figures 7–10. **7** *Archaeoteleia gracilis*, male (OSUC 163002), mesosoma, lateral view **8** *Archaeoteleia gracilis*, male (OSUC 163002), pronotum and mesopleuron, posterolateral view **9** *Archaeoteleia araucana*, male paratype (OSUC 163001), head, mesosoma, metasoma, lateral view **10** *Archaeoteleia astropulvis*, head, mesosoma, metasoma, lateral view. Scale bars in millimeters.

Comments. Masner (1968) suggested that the evolutionary origin of *Archaeoteleia* might have been Antarctic in origin, consistent with the distribution of extant species and the absence of fossil evidence of *Archaeoteleia* from other regions. The discovery of *A. astropulvis* from Myanmar and the presence of *Archaeoteleia* in Baltic amber indicate that the distribution of the genus was once found much farther north. We posit that *Archaeoteleia* in South America and New Zealand represent relictual populations of a once expansive distribution.



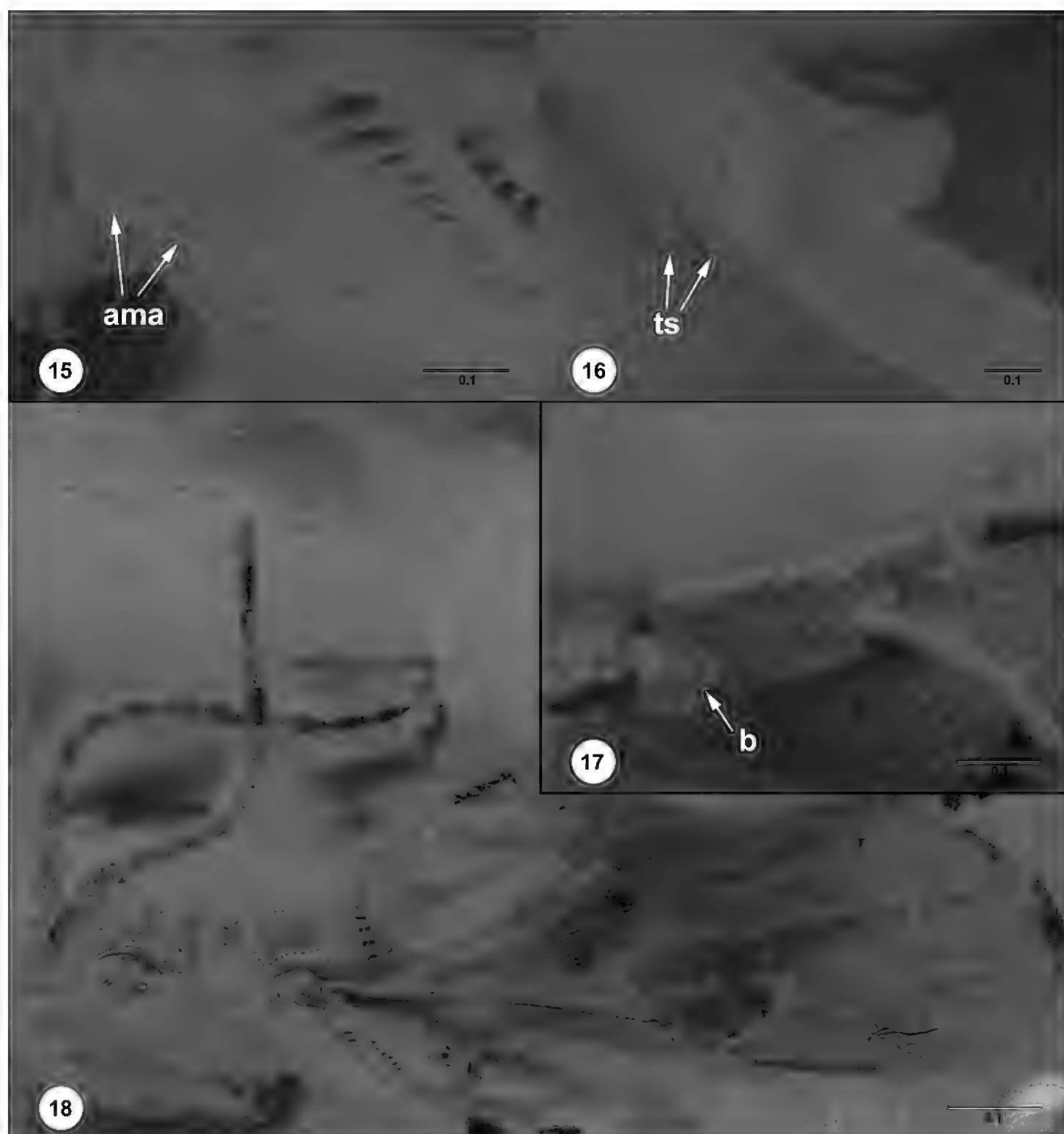
Figures 11–14. *Archaeoteleia pygmea* **11** male (OSUC 203907), habitus, lateral view **12** female (OSUC 146602), habitus, lateral view **13** male (OSUC 203907), mesopleuron, lateral view **14** female (OSUC 146602). Scale bars in millimeters.

Diagnosis of *Proteroscelio*

Proteroscelio can be identified by the following combination of characters: antennae 14-merous; clava in female antenna 8-merous and with pairs of basiconic sensilla arranged longitudinally; wings fully developed; 1Rs and M not intersecting in forewing.

Diagnosis of *Proterosceliopsis*

Proteroscelio nexus partially matches the diagnosis of *Proterosceliopsis* provided in Ortega-Blanco et al. (2014): 1Rs and M do not intersect, notauli are present and T1 is longitudinally striate. Their diagnosis stated that *Proterosceliopsis* has 6 visible tergites and a short, wide ovipositor. Based on the drawing and photograph of *Proterosceliopsis masneri* provided by Ortega-Blanco et al. (2014) (Figures 1, 6A) we offer an alternative interpretation, that the metasoma has 6 externally visible tergites and the apex is the partially extruded fusion of T7+8, as is found in scelionines with a *Scelio*-type ovipositor. In lieu of *P. nexus*, *Proterosceliopsis* can be differentiated from *Proteroscelio* by the fore wing not extending to the apex of the metasoma, a strongly transverse mesoscutellum and the presence of a horn on T1.



Figures 15–18. *Archaeoteleia* sp., male (USNMENT01223663) **15** mesopleuron, dorsolateral view **16** distal apex of metatibia, lateral view **17** fore wing venation, dorsal view **18** head and mesosoma, dorsolateral view. Scale bars in millimeters.

Diagnosis of *Bruescelio*

Ortega-Blanco et al. (2014) diagnosed *Bruescelio* on the basis of an antero-posteriorly compact shape of the head, a 6-merous clava, the absence of an occipital carina, 1Rs intersecting M in the fore wing, and T2 as the longest tergite. *Proteroscelio nexus* has T2 as the longest tergite (Figure 22), rendering this character unusable. The use of claval formula by Ortega-Blanco et al. (2014) for generic level diagnosis is potentially problematic because these authors did not clarify their criterion for differentiating

Key to Cretaceous platygastroid genera with 14-merous antennae (females)

- ## Character discussion

Wing Venation

Ortega-Blanco et al. (2014) used the abbreviations 2Rs and 3Rs for abscissae of the radial sector vein (Rs) in the fore wing. However, none of the taxa treated by them exhibit three abscissae in Rs, and thus these should be treated as 1Rs and 2Rs respectively. Our naming convention for these veins follows that of Ross (1937), Goulet and Huber (1993), and Dangerfiel et al. (2001).

Wing length

The length of the fore wing relative to the metasoma is often a consequence of metasomal length. Figures 24–25 and 26–27 illustrate two species of *Triteleia* Kieffer and two species of *Trichoteleia* Kieffer, respectively, in which the ratio of wing length to mesosomal length changes very little despite changes in the length of the metasoma. The shape of the body in scelionids is thought to be influenced by the shape of the egg in which the parasitoid develops; species that develop in elongate eggs tend to have an elongate habitus and species that develop in globular eggs tend to have a compact habitus. Furthermore, several characters are allometrically linked to body size, which is a direct function of host size and quality (Buffington and Polaszek 2009). Dramatically different adult parasitoid morphologies, within a population, can result from development within hosts of varying size or quality. Consequently, the length of the wing relative to the metasoma is a highly plastic character that is indicative of ancestry only to the degree that host choice is.

Mesoscutal pits

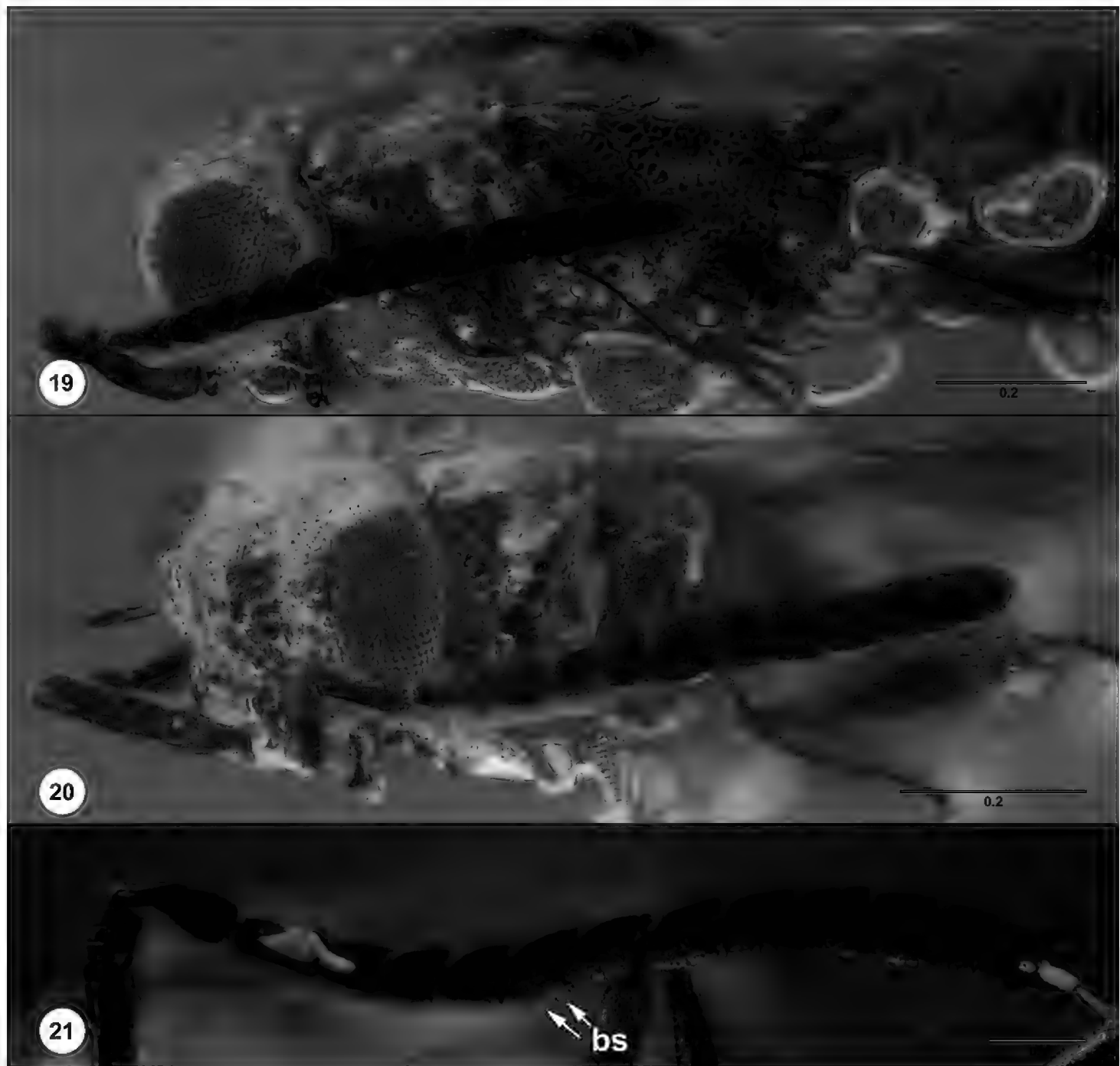
This term is unknown to us. It is not found in the Hymenoptera Anatomy Ontology nor is it used in platygastroid literature known to us and we deduce that Ortega-Blanco et al. (2014) were referring to the posterior scutellar sulcus (Figure 22), which is indicated by cells in almost all Scelionidae.

Horn on T1

The presence of a horn on T1 is often highly variable within genera (e.g. *Idris* Förster, *Inostemma* Haliday, *Probaryconus* Kieffer), and even within a species (e.g. *Trichoteleia janus* Talamas). We consider its use as a generic character to be reasonable only when supported by congruence with other characters.

Metasomal sculpture

The value of metasomal sculpture as a generic character is an extreme rarity in Platygastroidea and we know of only one instance where metasomal sculpture has real diagnostic power at the generic level: T3 in *Dvivarnus* Rajmohana & Veenakumari. The presence of striation on T1 is of little use at the generic level because the vast majority of platygastroids have T1 longitudinally striate to some degree, and within a genus there may be closely related species that differ by this character.



Figures 19–21. *Proteroscelio nexus*, female holotype (USNMENT01197245) **19** head and mesosoma, lateral view **20** head and mesosoma, anterolateral view **21** antenna, ventral view. Scale bars in millimeters.

***Proteroscelio nexus* Talamas, sp. n.**

<http://zoobank.org/278008AB-A3DF-4143-923E-A04D5C172C1A>

http://bioguid.osu.edu/xbiod_concepts/407637

Figures 19–23

Description. Female body length: 1.50 mm (n=1).

Head. Hyperoccipital carina: absent. Number of antennomeres: 14. Facial striae: absent. Frontal depression: absent. Malar sulcus: absent. Orbital carina: absent. Number of clavomeres: 8. Lengths of flagellomeres: approximately equal to maximal width, except A14 distinctly longer than wide. Swelling along inner orbit of compound eye: absent. Anterior margin of occipital carina: crenulate. Occipital carina: present.

Mesosoma. Pronotal suprahumeral sulcus: indicated by lines of cells. Transverse pronotal carina: present. Setation of lateral axillar region: absent. Notaulus: percurrent.



Figure 22. *Proteroscelio nexus*, female holotype (USNMENT01197245) habitus, dorsal. Scale bar in millimeters.



Figure 23. *Proteroscelio nexus*, female holotype (USNMENT01197245) habitus, ventral. Scale bar in millimeters.

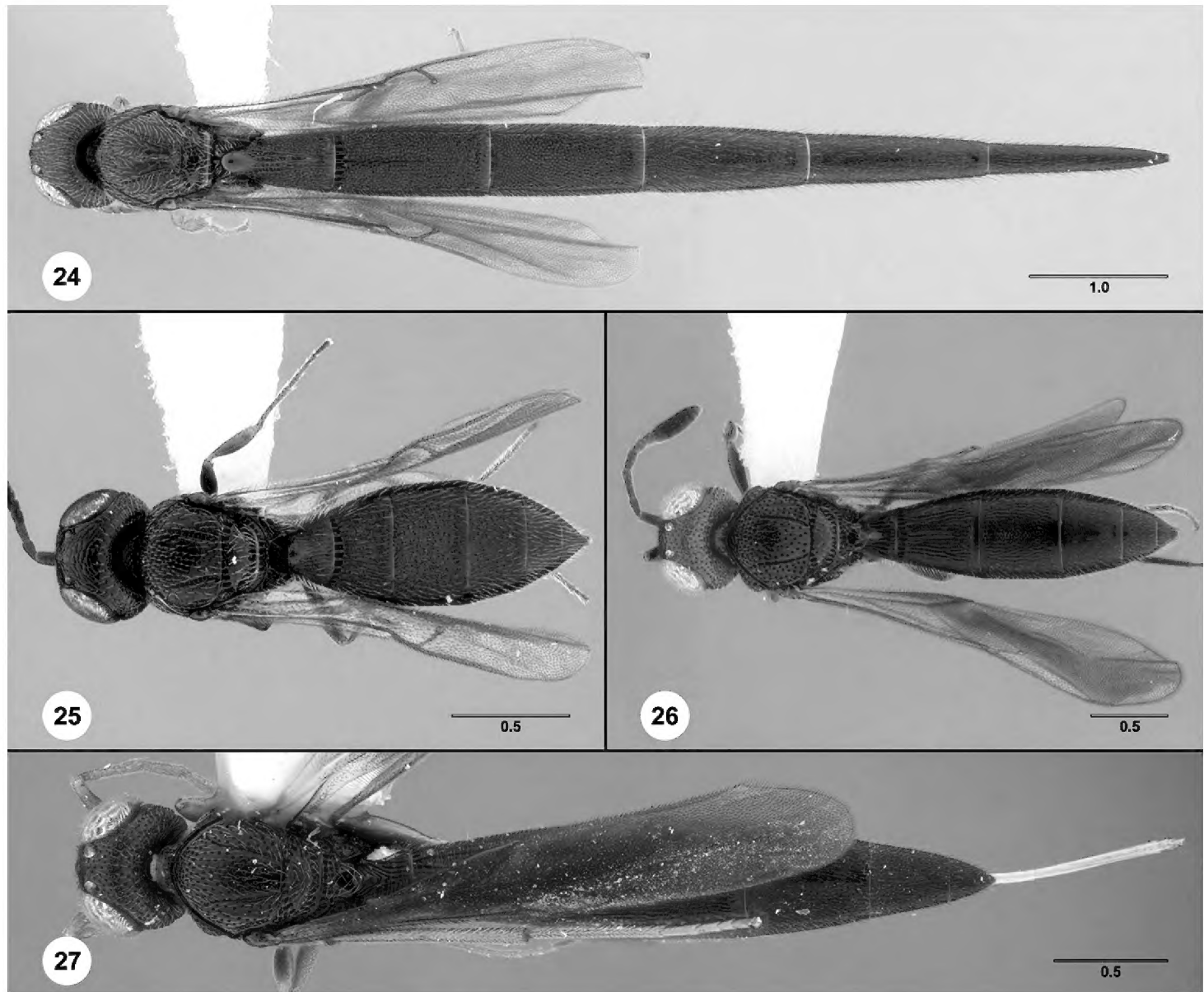


Figure 24–27. **24** *Triteleia* sp., female (OSUC 225498), dorsal view **25** *Triteleia* sp., female (OSUC 334149), dorsal view **26** *Trichoteleia hemlyae* (CASENT 2132833), female holotype, dorsal view **27** *Trichoteleia carinata* (USNMENT01109593), female, dorsal view. Scale bars in millimeters.

Macrosculpture of mesoscutellum: absent. Spines on mesoscutellar disc: absent. Metascutellum: differentiated from metanotal trough by line of 4 foveae directly posterior to mesoscutellum. Mesepimeral sulcus: present. Sculpture of dorsal metapleuron: transversely rugose. Posterior projection of the propodeum: present.

Metasoma. Sculpture of T2–T5: smooth posterior to foveae of antecostal suture. Horn on T1: absent. Antecostal sutures on sternites: externally indicated only on S2 as a line of costae. Antecostal sutures on tergites: indicated by cells on anterior T2–T4, T5 dubious.

Length of postmarginal vein: about equal to length of stigmal vein. Length of marginal vein: about equal to length of stigmal vein. Bristles on submarginal vein in fore wing: absent. Basal vein in fore wing: present. Bulla: present.

Diagnosis. *Proteroscelio nexus* is identifiable by the combination of strongly transverse T3–T5, percurrent notauli, and the serrate form of the clavomeres.

Etymology. This species is given the name “nexus”, derived from the Latin word for to “tie” or “bind” because this species shares characters between *Proteroscelio* and

Link to distribution map. <http://hol.osu.edu/map-large.html?id=407637>

Key to species of *Proteroscelio* (females)

- ## Acknowledgments

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Supplementary material I

URI table of HAO morphological terms

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Data type: Microsoft Excel Spreadsheet (.xls)

Explanation note: This table lists the morphological terms used in this publication and their associated concepts in the Hymenoptera Anatomy Ontology.

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